

Entrapment of an estuarine fish associated with a coastal surge barrier can increase the risk of mass mortalities



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ABSTRACT

Estuarine storm surge barriers are designed to prevent the flooding of human-developed landscapes. While such barriers may have a range of ecological impacts, including the fragmentation of aquatic habitats and the alteration of water quality, their impact on obligate estuarine fishes is largely unknown. The sparid, *Acanthopagrus butcheri*, was used as a model species to determine how surge barriers may influence the movements of solely estuarine species and fish kill events. Individual *A. butcheri* were monitored for one year using passive acoustic telemetry in the Vasse-Wonnerup Estuary (south-western Australia), in which fish kills occur regularly during summer and autumn. Hydrological data and surge barrier operational information were used to make inferences on the movements and habitat use of *A. butcheri*. Individuals were largely restricted to the waters downstream of the surge barriers. The fish tended to occupy deeper sites in proximity to complex structure with the distribution also influenced by changes in salinity during the spawning period. A strong seasonal trend existed in the daily distance travelled by the fish and this was positively associated with the annual flow period. The majority of fish that successfully passed upstream through one of the surge barriers did so through a fishgate that operated outside of the spawning period. All those fish were then likely trapped with no downstream fish passage occurring in summer and autumn at a time when water quality was characterised by low dissolved oxygen and cyanobacterial blooms. The surge barrier therefore acts as a seasonal trap and increases the risk of mass mortalities. Given a projected increased need to combat flooding and storm surges associated with climate change in low-lying coastal areas, the study highlights the necessity of ensuring that the life-cycles and movement requirements of estuarine fishes are considered in the design and operation of coastal flood mitigation structures.

1. Introduction

Estuaries and associated habitats including coastal deltas and tidal wetlands are of great ecological value (Hoellein et al., 2013; Sheaves et al., 2014; Tweedley et al., 2016a). Owing to their high productivity and location at the interface of freshwater and marine ecosystems, these systems are also often the centres of urban, industrial and agricultural development, which has resulted in estuaries being the most degraded of all marine ecosystems (Jackson et al., 2001; Gedan et al., 2009; Potter et al., 2015a). One of the major anthropogenic impacts on coastal and estuarine ecosystems has been the construction of flood mitigation barriers (or ‘surge barriers’) that can severely alter the hydrology (Lotze et al., 2006; Du et al., 2017) and may have wide-ranging ecological impacts (Pollard and Hannan, 1994; Poff et al., 1997; Lotze et al., 2006;

Arthington, 2012; Boys et al., 2012).

Estuarine surge barriers prevent upstream inflow while enabling downstream movement of freshwater; thus mitigating the risk of flooding from tidal and storm surges. However, they are known to fragment and cause degradation of habitats (Pollard and Hannan, 1994), alter water quality (Gordon et al., 2015) and may impede the movement of aquatic fauna, which may reduce species diversity and abundance (Boys and Pease, 2017). Despite this, few studies have assessed the impact of estuarine barriers on non-diadromous estuarine fish species, such as how they may effect migration patterns or population viabilities. Such an understanding is particularly important for fishes that complete their life-cycle within estuaries and thus their populations are generally not able to be readily replenished from stocks outside of the estuary (Potter et al., 2015b).

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Microtidal estuaries (tidal range < 2 m) with highly seasonal freshwater discharge can have a long hydrological residence time (e.g. months to years; Tweedley et al., 2016a) in comparison to macrotidal systems. These characteristics make microtidal estuaries particularly susceptible to environmental perturbations, including toxic phytoplankton blooms and/or hypoxia (Tweedley et al., 2016b; Warwick et al., 2018). Microtidal estuaries thus represent ideal systems to model and investigate the effects of anthropogenic stressors on estuarine fishes (Tweedley et al., 2017b).

The sparid *Acanthopagrus butcheri* (Black Bream) is a solely estuarine species that attains a maximum total length (TL) of 600 mm and can live for up to 30 years (Morison et al., 1998). It is an important target for recreational anglers in the estuaries of southern Australia and, in some estuaries, also contributes to commercial fisheries (Jenkins et al., 2010; Smith et al., 2014). *Acanthopagrus butcheri* may be highly mobile, with some individuals recorded moving > 1000 cumulative km per year; regularly travelling the length of estuaries (Williams et al., 2017). However, the life-cycle is generally completed within its natal estuary, with individuals thus exposed to environmental perturbations within estuaries should they arise (Cottingham et al., 2014, 2016). *Acanthopagrus butcheri* is thus an appropriate model species to investigate how the movement and distribution of an obligate estuarine fish species may be impacted by surge barriers.

In recent decades, hypoxia and toxic algal bloom events have increased in estuaries in southern Australia due to eutrophication, reduced rainfall and the subsequent reduction in freshwater discharge (Valesini et al., 2017). These events often develop in the upper regions of estuaries during summer and autumn; directly overlapping with the known habitats of *A. butcheri* (Hoeksema et al., 2006; Hallett et al., 2016). The presence of anthropogenic barriers may prevent mobile species, such as *A. butcheri*, avoiding those adverse conditions. While there have been several acoustic tracking studies on this species to determine its habitat use (Hindell et al., 2008; Sakabe and Lyle, 2010; Williams et al., 2017), as with many other species globally, none of those have specifically examined how the presence of surge barriers may exacerbate the impacts of environmental degradation on the species.

Overall, this study aimed to determine the key environmental factors that explain the movement patterns and distribution of *A. butcheri* within the lower portions of the Vasse-Wonnerup Estuary system in south-western Australia. The study also aimed to determine the hydrological and barrier operational conditions that explain the patterns of passage of fish through the Vasse and Wonnerup surge barriers. It was hypothesised that the surge barriers prevented freedom of fish passage, which would, in turn, increase the species' exposure to localised declines in water quality and therefore its susceptibility to fish kill events.

2. Materials and methods

2.1. Study site

The Vasse-Wonnerup Estuary is a shallow, intermittently-open system located near the town of Busselton, Western Australia (Brearley, 2005) (Fig. 1). The estuary is Ramsar Convention listed for its value to migratory birds, however, the estuary and its catchment have been extensively modified by anthropogenic activities (Tweedley et al., 2017a; Hart, 2014). The system experiences periods of gross eutrophication (Brearley, 2005) and fish kill events have occurred regularly, with at least nine such events occurring between 1984 and 2013 (Lane et al., 1997; Hart, 2014). Anoxia, high water temperatures, hypersalinity, macroalgal blooms and/or toxic phytoplankton have all been considered the causes of these events (Lane et al., 1997; Hart, 2014).

Permanent surge barriers were installed in 2004 at the junctions of both the Vasse and Wonnerup estuaries and the Wonnerup Inlet

(current structures are each of the same design) to prevent seawater intrusion (Figs. 1 and 2). Fish kill events over the past two decades have predominantly occurred within the proximity of the Vasse surge barrier (Fig. 1) and consisting of the deaths of up to ~40,000 individuals of *A. butcheri* along with the mugilids *Mugil cephalus* and *Aldrichetta forsteri* (Tweedley et al., 2014). The surge barriers allow one-way downstream movement of water during the peak winter-spring flow period. During summer and autumn, the surge barriers close and slot boards are installed that block the connection between the Wonnerup Inlet and the Vasse Estuary upstream (to maintain upstream water levels to ensure habitat for wading birds), however, a fish-passage chute (4 m × 0.4 m (L × W), hereafter referred to as the 'fishgate') can be opened to an adjustable height with the aim of enabling upstream and downstream fish movement through the structure (Fig. 2).

2.2. Receiver deployment and fish tagging

Nine VR2W (VEMCO) acoustic receivers (69 kHz) were deployed in March 2014; five within the Wonnerup Inlet (downstream of the Vasse and Wonnerup surge barriers), two upstream of the Vasse surge barrier and two upstream of the Wonnerup surge barrier (Fig. 1). Receivers were fastened to 10 mm diameter nylon rope and suspended below a 200 mm diameter styrene float that was attached to 4.5 kg galvanised sand anchors. Range testing for detections at receivers was performed using a V9-2L range test tag (transmitted an acoustic signal every 12 s) that was suspended in the middle of the water column at progressive distances of 25 m from each receiver (starting at 0 m), up to a maximum distance of 100 m for a period of 5 min. To elucidate the detection range of each receiver, a comparison was made between the actual and the expected number (i.e. 25 detections) of detections recorded at each progressive distance.

Forty-one *A. butcheri* were captured for internal acoustic and external T-bar tagging from the Wonnerup Inlet using a combination of rod and line and a 21 m seine net. Mean size of the fish implanted with V9-2L VEMCO acoustic transmitters was 291 mm TL ($\pm$ 5.95 S.E., TL range = 250–393 mm). Acoustic transmitters (weight = 4.7 g) were programmed to transmit at a random interval of between 60 and 120 s (estimated tag life = 382 days). The mean and maximum transmitter weight to fish weight ratio was ~1.1% and 2.2%, respectively. Prior to tagging, *A. butcheri* were placed into an aerated 110 L insulated holding tank and anaesthetised by emersion in 3 mg/L AQUI-S® anaesthetic-estuary water solution and monitored until loss of movement and equilibrium was observed. Each fish was then inverted and placed into a sponge cradle with its gills being constantly irrigated with the AQUI-S® solution and a transmitter implanted by making an incision in the abdominal wall and inserting it into the peritoneal cavity. The incision was closed with a single suture (glucanate monofilament size 4/0) and swabbed with an antibiotic solution (Betadine®). An external T-bar tag (Hallprint Australia®) was placed laterally to the dorsal fin to enable identification and release of tagged fish captured by recreational fishers. Tagged fish were then placed in an aerated 110 L recovery tank and monitored until full equilibrium and normal behaviour was observed at which time they were released at the site of capture (generally within 10–15 min post-surgery).

2.3. Environmental variables

In order to determine the drivers of the spatial and temporal changes in the residency and movement patterns of *A. butcheri* throughout the Vasse-Wonnerup Estuary, a suite of environmental and physical variables were collected over the study period. The variables that were measured included the known physicochemical drivers of the movement and habitat use of this species, or those that could indirectly influence them. They included; day of experiment (for seasonality of life history), flow regime (and operational status of the surge barrier, see below), habitat complexity, salinity (conductivity), water

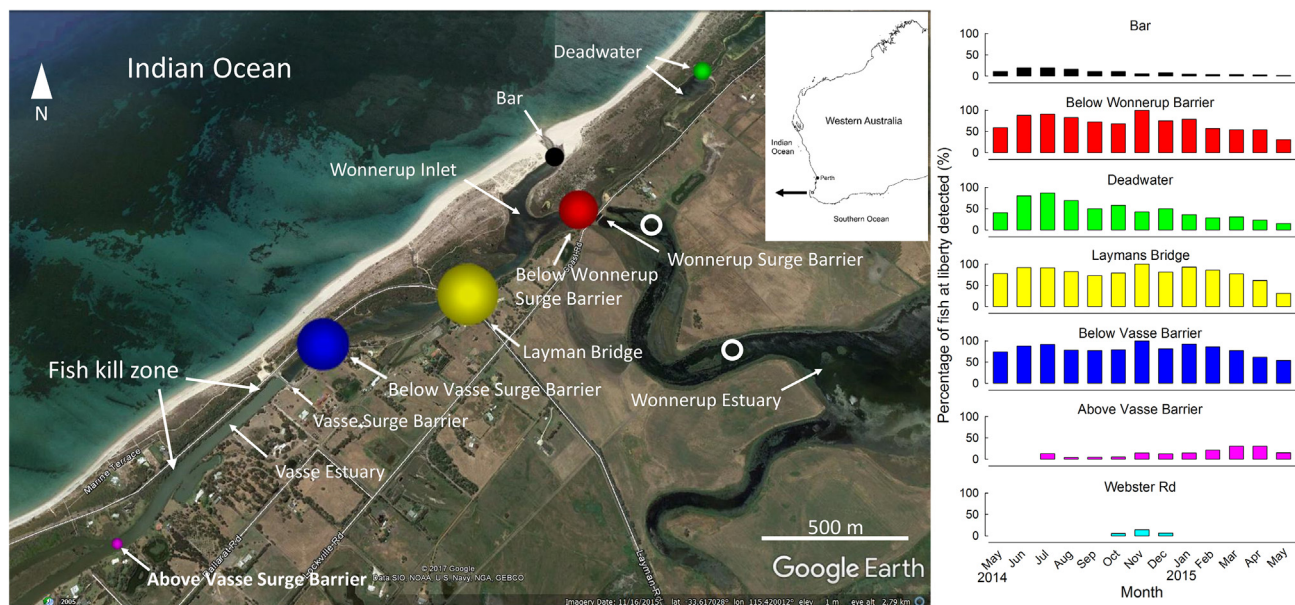


Fig. 1. The location of the acoustic receivers in the Vasse-Wonnerup Estuary system in south-western Australia. The area of each circle is proportional to the overall residency of *Acanthopagrus butcheri* throughout the study at each receiver. Bar charts represent the percentage of all fish still at liberty in the array that were detected at individual receivers in each month. N.B. Webster Rd receiver was located further upstream in the Vasse Estuary and outside of the map and had a very low overall mean residency of 0.03 ± 0.03). The receivers above the Wonnerup surge barrier had no valid detections and are shown as white circles. The major fish kill zone upstream of the Vasse Surge Barrier is highlighted.

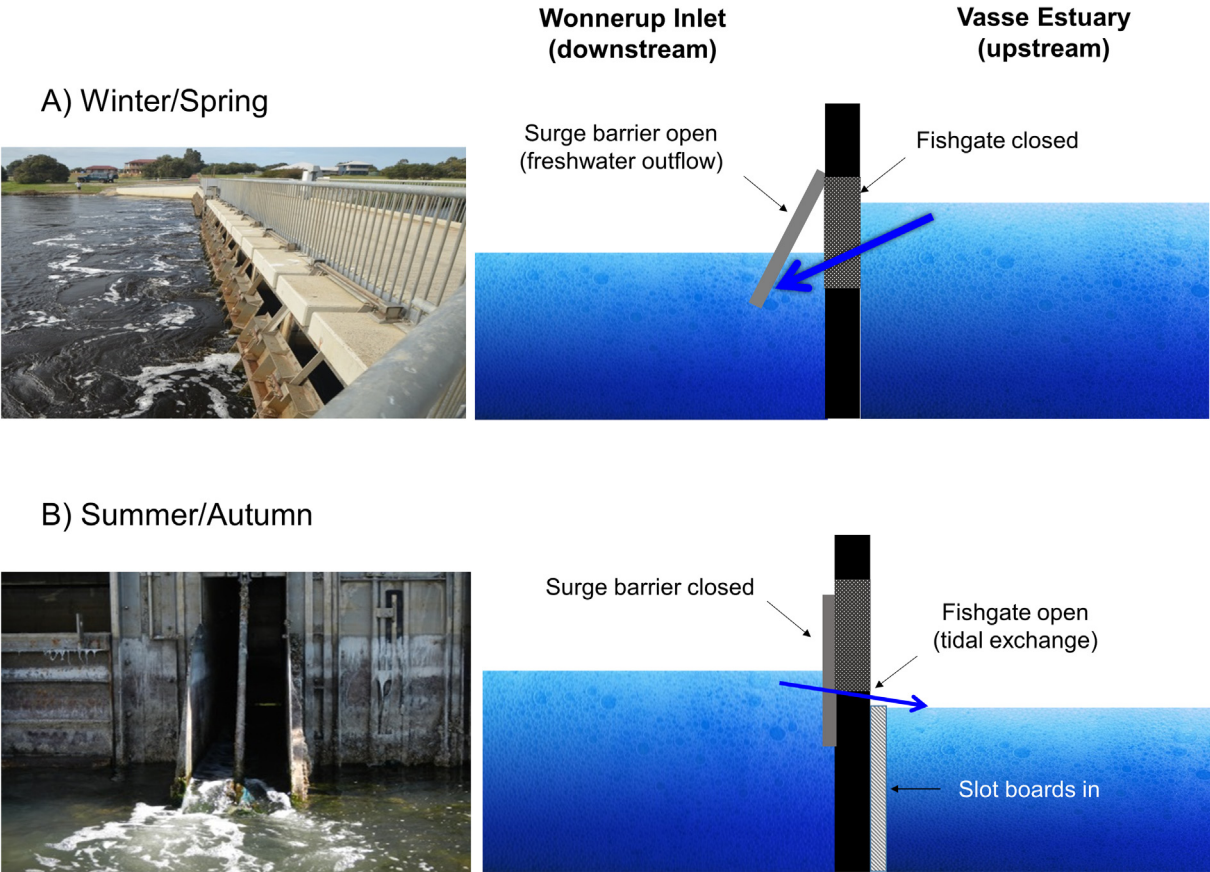


Fig. 2. A) Conditions at the Vasse surge barrier during the high flow period in winter-spring 2014 showing the one-way surge barriers pushed open (upper photo). B) Conditions at the barrier during summer-autumn when the fishgate is operational (lower photo, taken from the upstream side of the barrier). N.B. the slot boards in place either side of the fishgate) allowing water to flow upstream from the Wonnerup Inlet into the Vasse Estuary. N.B. the higher water level on the downstream side of the surge barriers during summer-autumn, the blue arrows represent direction of flow.

Table 1

Description of the variables used in the GAMM and GAM analyses of spatial distribution and movement of *A. butcheri* in the Vasse-Wonnerup Estuary, south-western Australia.

Variable name	Variable type	Variable code
Response variables		
1) Daily number of individuals detected at receivers	Discrete	–
2) Daily number of individuals detected at the receiver downstream of the Vasse surge barrier	Discrete	–
3) Daily distance moved by fish within the array	Continuous	–
Fixed explanatory variables (numbers in parenthesis denote the factor was included in modelling the respective response variable above)		
Vasse surge barrier status (1, 2, 3)	Nominal (open or closed)	Barrier
Connection of Vasse-Wonnerup to the ocean (1, 2, 3)	Nominal (open or closed)	Bar
Vasse check board status (1, 2)	Nominal (open or closed)	Boards
Complex habitat present near receiver (1)	Nominal (present or absent within 100 m radius of each receiver)	CS
Day of the study (1, 2, 3)	Continuous (smoothed, between 22nd May 2014 (i.e., day 1) and 24th February 2015 (i.e. day 279))	sTime
Mean depth of habitat around receivers (1)	Continuous (mean water depth around 100 m radius of each receiver)	Depth
Mean daily salinity at each receiver (1)	Continuous (smoothed)	sSal
Mean daily salinity at all receivers (3)	Continuous (smoothed)	sSal
Mean daily salinity at receiver below Vasse surge barrier (2)	Continuous	sSal
Distance (circuitous) of receiver from the ocean (1)	Continuous (smoothed)	sDist
Moon visibility (2, 3)	Continuous	Moon
Fish length (3)	Continuous	Length
Connection of Vasse-Wonnerup to the ocean: Tidal amplitude (1, 2, 3)	Interaction	Bar:Tide

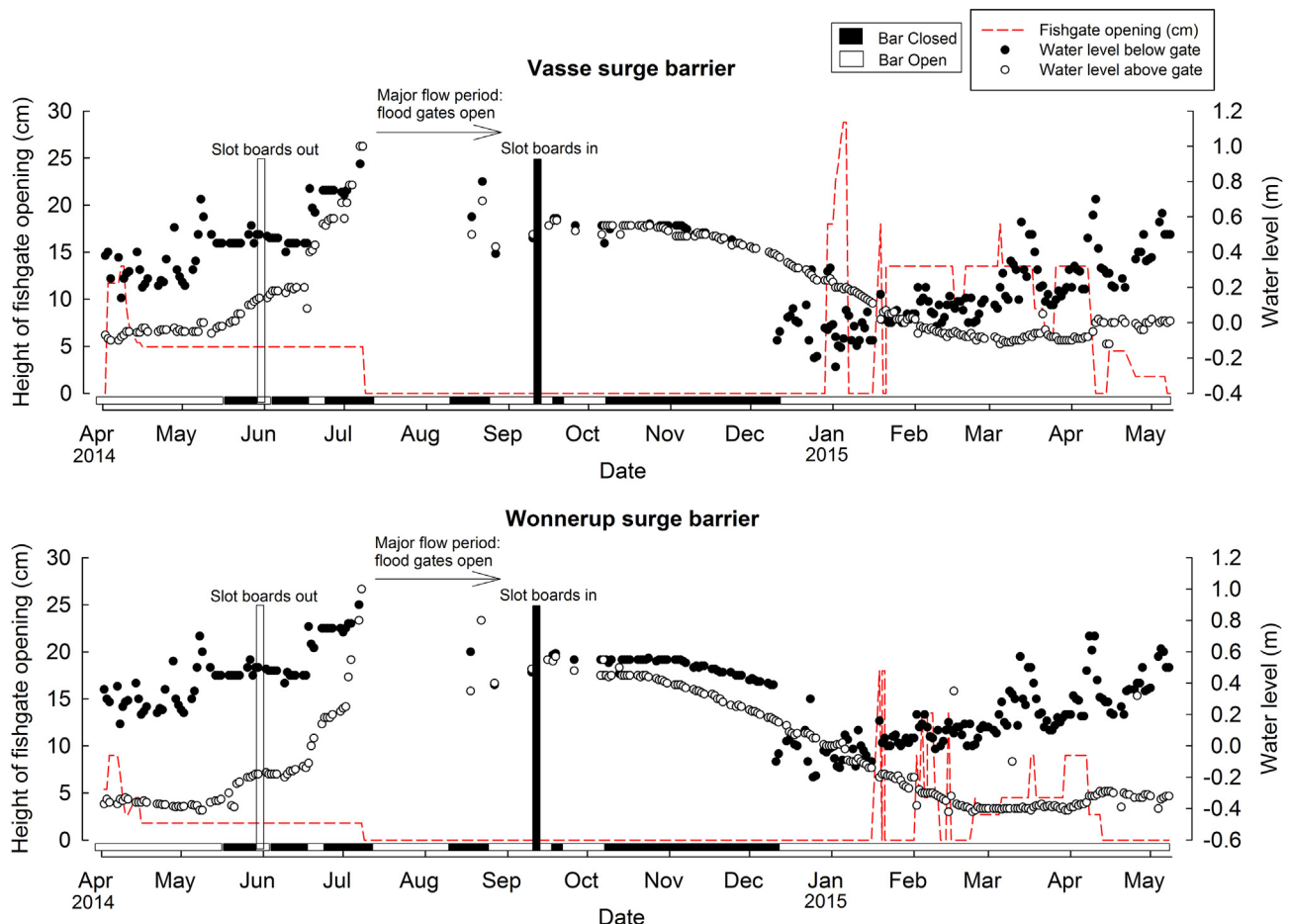


Fig. 3. Hydrological and operational conditions of the Vasse and Wonnerup surge barriers throughout the study period from April 2014–May 2015. The horizontal bars on the X axis represent the opening status of the sandbar to the Indian Ocean (i.e., either open (clear) and closed (black)). The two vertical bars on each graph indicate the date when the slot boards are removed or installed (i.e. when installed they completely block the flow of water through the surge barriers aside from the periods when the fishgates are open (with the fishgate opening gaps being denoted by the dashed line corresponding to the left hand y axis. See Fig. 2B)). The daily observed water levels upstream (clear circles), and downstream (black circles) of the surge barriers are provided (corresponding to the right hand y axis). N.B. the higher water levels downstream from late January 2015 onwards at the surge barriers when their fishgates were operational. Note also the onset of the major winter-spring flow period in early July 2014 when the main surge barrier gates are pushed open (see Fig. 2A).

temperature, tidal regime and amplitude, moon phase and fish size (Hindell, 2007; Hindell et al., 2008; Sakabe and Lyle, 2010; Cottingham et al., 2014, 2016; Williams et al., 2017) (Table 1).

The status of the sandbar at the mouth of the estuary was monitored on a daily basis and was recorded as “open” or “closed” depending on the accumulation of sand. The dates when the Vasse and Wonnerup surge gates were ‘forced’ open by the downstream flow of freshwater were also noted, along with the dates when the slot boards were put in place on the surge gates (see Fig. 2). Daily records of the vertical height of the opening in the fishgates were also obtained from the operators of the surge barrier (C. Piggott, Water Corporation of Western Australia, pers. comm.). Conductivity and water temperature loggers (Odyssey™) were deployed on each receiver (at a depth of ~1 m) and were programmed to record both variables every 30 min.

Bathymetry and underwater structure were mapped throughout the Wonnerup Inlet array using a Lowrance HDS Gen 3 sonar (with a StructureScan HD transducer) mapping 30 m wide transects. The sonar log file produced was analysed in the ReefMaster PRO software package and was used to create structure and bathymetry maps to calculate the mean depth around each receiver (to a distance of 100 m) using the sidescan mosaic and volumes and areas add-ons. The sidescan mosaic map created was reviewed in order to estimate the amount of complex structure present (principally large woody debris) around the approximate detection radius of each receiver as this is known to influence the movement and distribution of *A. butcheri* (Hindell, 2007).

2.4. Determining the spawning period of *A. butcheri*

Gonadosomatic development of *A. butcheri* in the Vasse-Wonnerup Estuary was examined to determine whether temporal patterns in habitat use and movement was associated with reproductive activity. A total of eight sites in the mid-channel sampling of Wonnerup Inlet and the Deadwater (N.B. despite its name, the Deadwater refers to a region that does not receive direct freshwater flow and does not typically suffer from fish kill events) were sampled seasonally between February 2014 to May 2015 using sunken composite multifilament gillnets (Fig. 1). Additional samples of *A. butcheri* were collected monthly from the mid-channel sampling in the upper reaches of the Deadwater between October 2014 and September 2015. This site was chosen as previous research showed that *A. butcheri* remained relatively abundant in this area throughout the year (Tweedley et al., 2014) and, although it lacks riverine input, this site is located furthest ‘upstream’ from the entrance channel and thus, to some extent, parallels the region in a typical estuary where *A. butcheri* would spawn in south-western Australia (Sarre and Potter, 1999; Cottingham et al., 2014).

Each individual *A. butcheri* that was retained for gonad development (see Fig. 4) was measured to the nearest 1 mm TL, weighed to the nearest 0.01 g and sexed on the basis of macroscopic examination of its gonads. The gonads were weighed to the nearest 0.01 g and assigned to one of the following stages on the basis of their macroscopic appearance: I/II = virgin or resting, III = developing, IV = maturing, V = prespawning/mature, VI = spawning, VII = spent and VIII = recovering spent (Laevastu, 1965; Sarre and Potter, 1999). The trends exhibited by the prevalence of the different stages in ovarian development in sequential months, allied with those of mean gonad weights were used to determine the spawning period and the approximate time of peak spawning. The monthly trends in gonad weight of female and male *A. butcheri* were compared by standardising for length as gonad weight is highly dependent on fish size; with larger fish generally having proportionately larger gonads than smaller individuals (Gonor, 1973). In this analysis, only fish ≥ 160 mm, the approximate L_{50} (length at which 50% of fish are mature), were used.

2.5. Residency and movement

Mean residency of *A. butcheri* at each receiver was calculated as the

mean proportions of all days at liberty that each fish was detected at a specific receiver. This analysis excluded fish detected < 2 times at a receiver in a day and was truncated to start on 22nd May 2014 (seven days after the last tagging event) to account for any unusual behaviour that tagged fish may have displayed post-tagging, and end on 20th May 2015 to reduce bias from uneven sample sizes associated with detection failures at some locations after this date. Monthly residency at each receiver was also determined to explore temporal trends in residency throughout the study period. This was calculated as a proportion of the total number of tagged fish detected at a receiver in a month compared to the total number of tagged fish detected anywhere in the array in that month.

Daily movement of each tagged fish was calculated using a circuitous distance matrix that consisted of the total minimum distances required to travel between each receiver using VTrack version 1.11 (Campbell et al., 2012) in R (RStudio Team, 2016). The relationship between total fish length and the average daily distance travelled by individuals during their time at liberty was analysed using a Pearson product-moment correlation.

2.6. Passage through the surge barriers

To determine the hydrological and fishgate operational conditions under which each fish traversed upstream through the surge barriers, daily observations were made of several factors and matched to passage events that were recorded by the acoustic array (i.e. a fish being detected at the receiver downstream of the surge barriers, then being detected upstream, or vice versa). These included whether each surge barrier was open or closed (i.e. associated with downstream freshwater discharge), the height of the fishgate opening, and the daily observation of the difference in water level height immediately upstream and downstream of the surge barriers.

2.7. Factors explaining distribution and movement

Generalised additive mixed models (GAMMs) were employed with a Poisson error distribution to determine which of the environmental and surge barrier operational factors explained the variation in the daily number of individual *A. butcheri* detected at receivers throughout the Wonnerup Inlet. The explanatory variables included in the GAMMs are outlined in Table 1 with receiver number (ID) included as a random factor. We initially checked for correlation between environmental factors and found water temperature was strongly positively correlated with day of experiment ($r = 0.92$). Temperature was removed from the analyses as *A. butcheri* is known to undertake seasonal movement patterns corresponding to its annual breeding period (Hindell et al., 2008; Sakabe and Lyle, 2010; Williams et al., 2017), which was also determined in the current study, and the temporal movement patterns had more direct management implications than the influence of temperature. In order to determine which factors increased the probability of fish congregating below the Vasse surge barrier (i.e. within the zone of recent fish kills), a separate analysis was undertaken to determine the factors that best explained the variation in the daily number of individual *A. butcheri* detected at the receiver downstream of the Vasse surge barrier. Generalised additive models (GAMs) were employed with a negative binomial error distribution to account for over-dispersed count data with a suite of explanatory variables initially included in the global model (Table 1). The factors that best explained the mean daily distance moved by fish within the array were determined using a GAMM (with a Gaussian error distribution) with fish ID included as a random effect. The mean daily distance was $\log(x + 1)$ transformed prior to analysis and a suite of explanatory variables initially included in the global model (Table 1).

For all of the above models, correlograms were produced to examine the level of first order temporal autocorrelations (day of experiment) in the time series data. Autocorrelation with a one-day lag was detected in

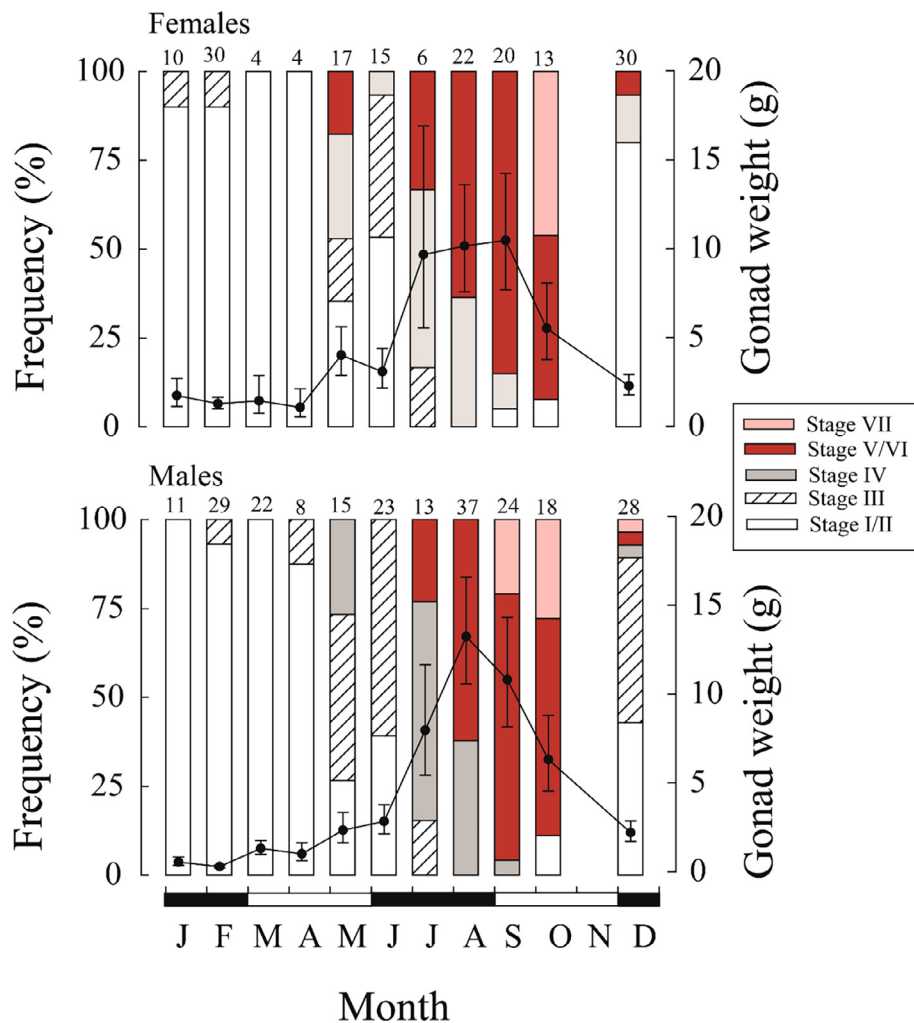


Fig. 4. Percentage frequency of occurrence in successive months of sequential stages in gonadal development and mean gonad weight (with 95% confidence intervals) in female and male *Acanthopagrus butcheri* of lengths $\geq L_{50}$ at maturity in the Vasse-Wonnerup Estuary. Sample size for each month is shown.

all datasets and an autocorrelation term (corAR1) was added to account for the lack of temporal independence of the telemetry data (Pinheiro and Bates, 2000). Day of experiment was added as the time covariate for all models, and grouping factors of receiver ID for the fish distribution GAMM and fish ID for the daily distance moved GAMM, respectively.

Model selection

In order to determine the most parsimonious model, global models were first fitted by including all terms and interactions (outlined above and in Table 1), and nested models were compared using Akaike information criterion corrected for small sample size (AICc), as described by Zuur et al. (2009) and Wood (2006). A sub-set of models were generated and ranked that were within four AICc of the best model (Burnham and Anderson, 2010), using the package MuMIn (Bartoń, 2013) in R (RStudio, 2016; version 0.99.893). The relative importance of each predictor variable (i.e. the selection probability that a given variable will appear in the AICc best model) was then determined by summing the AICc weights across all models within the top-ranked set that contained the variable (Burnham and Anderson, 2010). In order to examine the effects of smoothed explanatory variables, the best fitting GAMMs for the daily number and of fish detected at receivers in Wonnerup Inlet, and the daily distance moved, and the GAM for the number of fish detected below the Vasse Surge receiver were then fitted. Diagnostic residuals and quantile-quantile plots were visually analysed to ensure all assumptions of the GAMMs and GAM were met.

All GAMMs/GAMs detailed above were performed using the package mgcv (Wood, 2017) in R (RStudio, 2016; version 0.99.893).

3. Results

3.1. Range testing

Range tests revealed that the mean percentages of detections from the test tag at 25, 50 and 100 m distance from the receivers in the Wonnerup Inlet were $92.2 \pm 6.0\%$, $90.4 \pm 2.3\%$ and $85 \pm 5.8\%$, respectively. Detection ranges were much lower in the receivers located upstream of the surge barriers with the mean percentage of pings detected at 25, 50 and 100 m distance being $93.6 \pm 3.6\%$, $45.9 \pm 28.1\%$, and 0% , respectively. Despite this variability, the detection radius of the receivers were sufficient to have a very high likelihood of detecting passing fish given the relatively small width of the inlet and estuaries where they were located (i.e., a maximum width of ~ 50 m at all receiver locations) (Fig. 1).

3.2. Environmental variables

The bar at the mouth of the Wonnerup Inlet was open to the Indian Ocean for 170 days of the study period with the sand bar becoming closed on six separate occasions. The longest period of closure occurred between October 6th to December 10th 2014 when it was physically excavated to enable tidal water exchange during summer and autumn

Table 2

Acanthopagrus butcheri that successfully traversed through the Vasse surge barrier during the study. N.B. *denotes those fish that used the fishgate to pass through the surge barrier. Also included is the passage date, the water level differentiation downstream compared to upstream of the barrier (positive = higher water levels on the downstream side), the status of the one-way surge barriers (i.e. open during high flow period), the gap width of the fishgate, and the date the fish was last detected in the array.

Fish ID	TL (mm)	Date first above barrier	Date last above barrier	Water level Δ D/S to U/S across barrier (m)	Surge barrier status	Vertical fishgate gap (cm)	Date last detected
14688	290	6/7/14	8/7/14	−0.05	Open	4.95	20/5/15
14726	370	7/7/14	29/12/14	−0.10	Open	4.95	29/12/14
14690	287	12/11/14	20/5/15	0.00	Shut	0.00	20/5/15
14701*	269	3/2/15	20/5/15	0.14	Shut	13.50	20/5/15
14709*	305	28/3/15	27/4/15	0.25	Shut	13.50	27/4/15
14715*	393	7/4/14	6/10/14	0.47	Shut	11.70	6/10/14
14729*	360	28/1/15	30/4/15	0.02	Shut	13.50	30/4/15

as a management measure to help improve water quality (Fig. 3). From the latter date, the system was open to the ocean until the study ceased on 20th May 2015 (Fig. 3). During periods when the sand bar was opened, variations in conductivity occurred corresponding to tidal influence (Supplementary Figs. 9–15). In the Wonnerup Inlet, the magnitude of variation in conductivity during tidally influenced periods was greatest at the most downstream receiver (i.e. the ‘bar’, Supplementary Fig. 9), and least at the ‘Deadwater’ receiver (Supplementary Fig. 12).

The impact of the surge barriers on conductivity was pronounced with a noticeable lack of tidal influence upstream of both the Wonnerup and Vasse surge barriers and consistently low salinities occurring between early July and November (Supplementary Figs. 11 and 15). Water temperature had similar temporal variation among receiver sites, declining between April and July, before steadily increasing to peak in early February 2015 (Supplementary Figs. 9–15).

3.3. Spawning period of *Acanthopagrus butcheri*

Nearly all female *A. butcheri* with lengths $\geq L_{50}$ at maturity possessed virgin or resting ovaries (stage I/II; Fig. 4) between January and April. The percentage frequency of occurrence of females with mature/spawning gonads (stage V/VI) increased from 0% in June to between 33 and 46% in July to October, before declining to 7% in December. The percent frequency of occurrence for sequential stages in testis development followed a similar trend to ovaries, with mature/spawning testes (stage V/VI) of males being greatest between July and October (Fig. 4). The mean gonad weight (standardised for a fish with a total length of 230 mm) of female *A. butcheri*, increased from < 1.8 g between January and April and from 2.1 g in June to ~10 g between July and September then declined to 2.3 g in December (Fig. 4). The mean gonad weights of male *A. butcheri* followed a similar trend, rising from 2.8 g in June to between 6.3 and 13.3 g in July and September then declined to 2.2 g in December.

3.4. Residency and daily movement

Thirteen of the 41 tagged *A. butcheri* were excluded from the calculation of residency and all models of residency or movement with environmental variables, with six of those excluded as they were not detected after the 22 May 2014 and seven excluded as they were detected for an extended and uninterrupted period (i.e., > 5 months) at a single receiver and were assumed to have either died or to have shed the tag. Two additional fish were excluded from the analysis of individual movements as no movements were recorded during the period due to either being detected for a short (< 10 day) period at a single receiver (fish 14692) or only being detected at the receiver upstream of the surge barrier after 22 May 2014 (fish 14715).

A total of 2,307,576 tag detections were received between 22nd May 2014 and 20th May 2015. No valid detections were recorded at the

receivers upstream of the Wonnerup surge barrier. The highest overall residency across the study period was recorded at Layman Road Bridge (0.61 ± 0.06) and below the Vasse surge barrier (0.51 ± 0.07) with the least frequented habitats both being upstream of the surge barrier i.e., Webster Rd (0.03 ± 0.03) and immediately above the surge barrier (0.1 ± 0.05) (Fig. 1). However, the temporal patterns in monthly residency at each receiver revealed a general declining trend of residency at all receivers after January 2015. The only exception was the receiver upstream of the Vasse surge barrier, which had an increasing proportion of tagged fish being detected from January to April 2015 (Fig. 1).

The mean daily distance moved by *A. butcheri* was $2.73 \pm 0.06 \text{ km.day}^{-1}$ with a maximum of 45 km recorded for fish ID14698 (264 mm TL) on 23 November 2015. There was no significant relationship between total length of the fish and the mean daily distance moved by individual *A. butcheri* (Pearson's correlation $r = -0.17$, $p = 0.40$).

3.5. Passage through the Vasse surge barrier

A total of seven *A. butcheri* were detected at one or both of the acoustic receivers upstream of the Vasse surge barrier throughout the study (Table 2, Supplementary Figs. 1–7). Two of these fish traversed during a period of high flow in early July 2014 when the surge barriers were forced opened by downstream flow (Fig. 2A) with one returning downstream after a period of two days; being the only *A. butcheri* that undertook a two way (upstream then downstream) passage through the barrier with the other six fish that traversed through last being detected upstream of the barrier (Fig. 2A, Supplementary Figs. 1 and 2). Of the 17 *A. butcheri* that were still being detected anywhere in the array after December 2014, five (i.e., 29%) were detected only above the Vasse surge barrier for the remainder of the study period.

Four of the seven *A. butcheri* that traversed through the Vasse surge barrier did so during the period when the slot boards were in place and the fishgate was operational. Moreover, each passed through the gate when the daily observation recorded higher water levels on the downstream side of the surge barrier (difference in water level range of 0.02–0.47 m) (Table 2, Supplementary Figs. 4–7). The vertical gap in the fishgate when the four fish traversed ranged from 11.7 to 13.5 cm (Table 2). One fish appeared to passage upstream during a period when both the surge barrier and fishgate were shut; likely a result of either a translocation by a recreational fisher or a bird (Table 2, Supplementary Fig. 8).

3.6. Factors explaining distribution and movement

Model selection revealed the daily number of fish detected at each receiver was best explained by the GAMM containing the factors: mean depth around receiver (positive), receiver being in proximity to a major complex structure (positive), smoothed effect of time (day of the

Table 3

Importance (i.e., probability of selection in best fitting model) of predictor variables for the models explaining: 1) The number of *Acanthopagrus butcheri* detected daily at receivers within the Wonnerup Inlet, 2) the number of *A. butcheri* detected daily at the receiver below the Vasse surge barrier, and 3) the mean daily distance moved by *A. butcheri*. N.B. See Table 1 for variable codes and text for more details.

Response variable	Explanatory variable	Importance
1) Daily detections (Wonnerup Inlet array)	Depth	1.00
	CS	1.00
	sTime	1.00
	sSal	0.87
	Boards	0.27
	Barrier	0.13
	Bar	0.10
2) Daily detections (below Vasse surge barrier)	sTime	1.00
	Barrier	1.00
	Boards	0.69
	Bar	0.32
	sSal	0.27
	Moon	0.19
3) Mean daily distance moved	sTime	1.00
	Barrier	1.00
	sSal	0.23
	Moon	0.15

Table 4

Outputs of the best fitting models for the: 1) Generalised additive mixed model (GAMM) for the daily detections across the entire Wonnerup Inlet, 2) Generalised additive model (GAM) for the daily detections below Vasse surge barrier, and 3) GAMM for the mean daily distance moved. N.B. see Table 1 for variable codes. Bold *p* values indicates significant at $p < 0.01$.

Response variable		Estimate	Std. Error	t value	Pr(> t)
1) Daily detections (Entire Wonnerup Inlet array)	(Intercept)	−0.500	0.358	−1.398	0.162
	Depth	1.788	0.423	4.224	< 0.001
	CS	0.912	0.161	5.655	< 0.001
	edf		Ref.df	F	<i>p</i> -value
	sTime	1.00	1.00	153.38	< 0.001
	sSal	2.822	2.822	3.719	0.030
2) Daily detections (below Vasse surge barrier)	Estimate	Std. Error	t value	Pr(> t)	
	(Intercept)	2.244	0.077	29.093	< 0.001
	Barrier	0.180	0.071	2.554	0.010
	Boards	0.100	0.079	1.209	0.228
	edf		Ref.df	F	<i>p</i> -value
	sTime	3.988	3.988	10.6	< 0.001
3) Mean daily distance moved	Estimate	Std. Error	t value	Pr(> t)	
	(Intercept)	0.160	0.049	3.253	0.001
	Barrier	0.250	0.037	6.774	< 0.001
	edf		Ref.df	F	<i>p</i> -value
	sTime	7.645	7.645	6.774	< 0.001

experiment), and mean salinity (Tables 3 and 4, Supplementary Table 1). Fish detection probability declined throughout the study period (Fig. 5A). Salinity was weakly associated with daily number of detections in the Wonnerup Inlet with detections peaking at 25–30 $\mu\text{S.cm}^{-1}$ (Fig. 5B). Model selection revealed that the daily number of fish detected at the receiver below the Vasse surge barrier was best explained by the GAM containing the factors: surge barrier opening (positive effect of being open during river flow period), and smoothed effect of time (day of the experiment) (Tables 3 and 4, Supplementary Table 1). Probability of fish being detected at the receiver below the Vasse surge barrier peaked between approximately

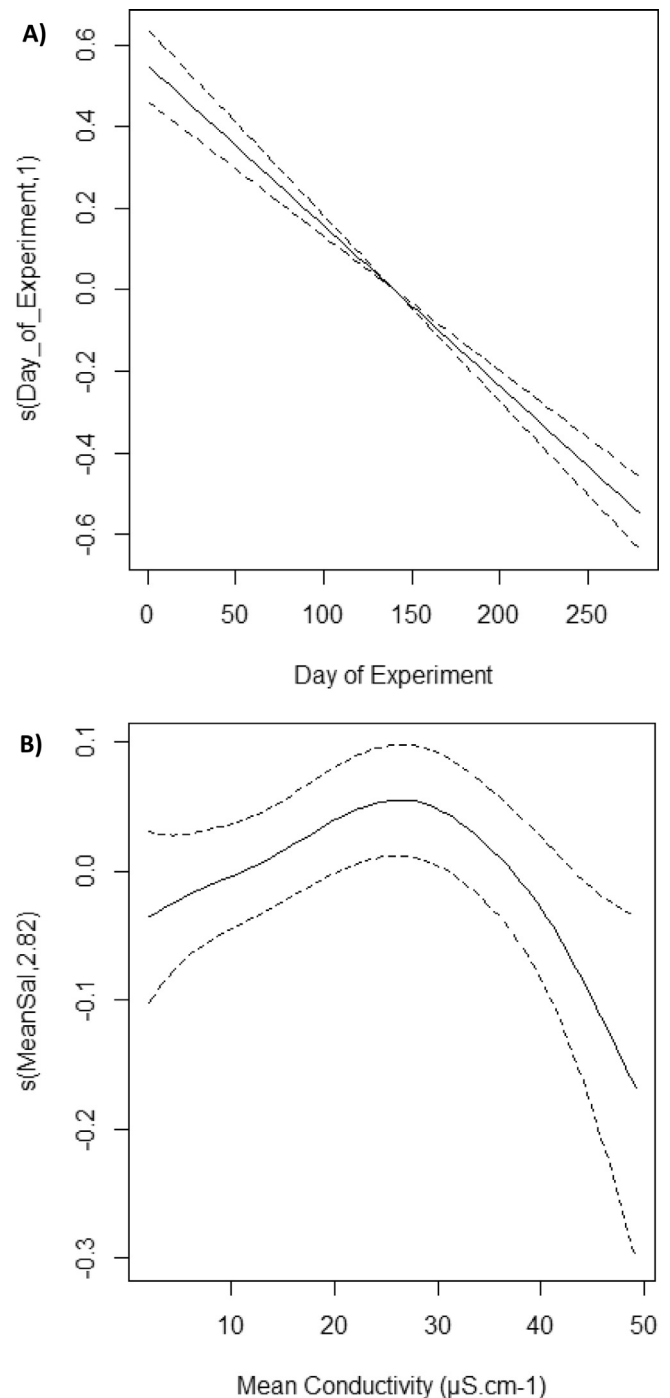


Fig. 5. Smoothing curves for the effects of time (day of study) and salinity (conductivity) on the daily number of *Acanthopagrus butcheri* detected throughout the Wonnerup Inlet from the best fitting generalised additive mixed-effects model.

days 70 and 130 of the study (corresponding to the period between early August and early October) (Fig. 6).

The daily distance moved by individual fish during the study period was positively associated with the status of the surge barrier (a positive effect of being open during river flow period) and smoothed effect of time (day of the experiment) (Tables 3 and 4, Supplementary Table 1). Clear peaks in movement occurred approximately between days 70–100 (i.e. August to September) and a more modest peak occurring approximately between days 150–170 (i.e. late October to November) (Fig. 7).

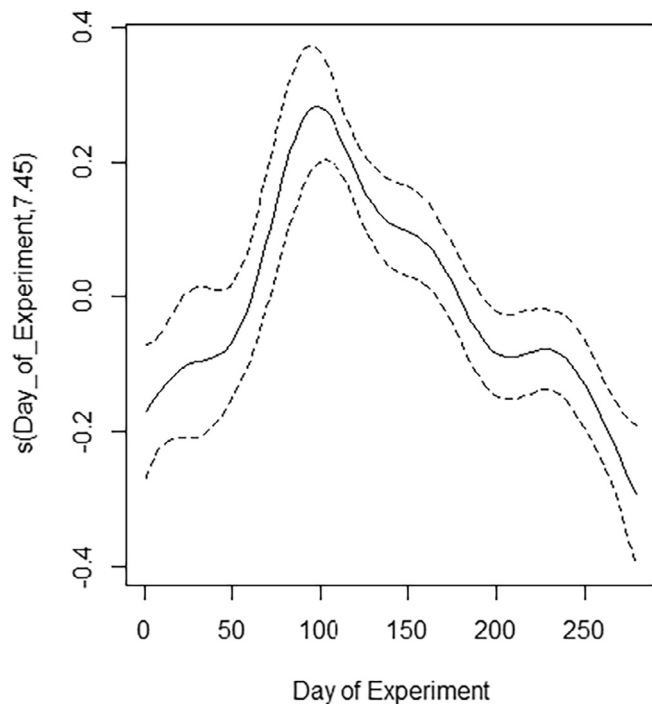


Fig. 6. Smoothing curve for the effect of time (day of study) on the daily number of tagged *Acanthopagrus butcheri* detected below the Vasse Surge gate from the best fitting generalised additive mixed model.

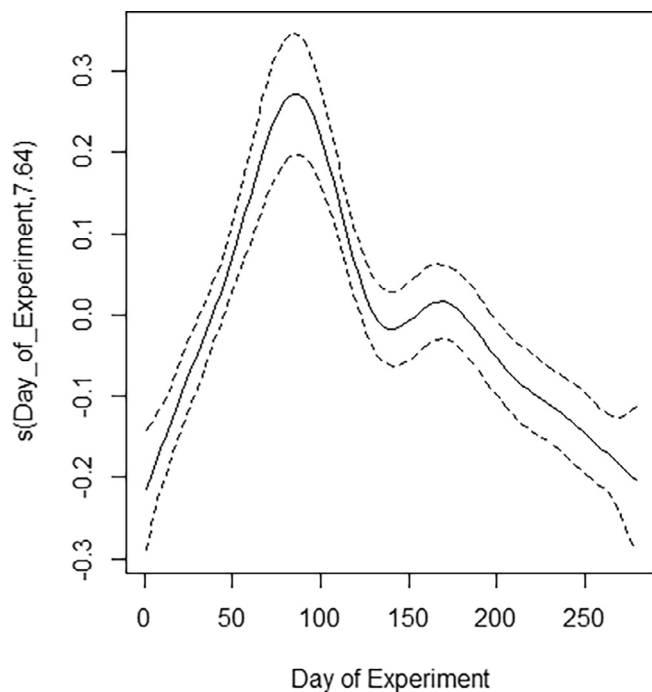


Fig. 7. Smoothing curve for the effect of time (day of study) on the daily distance moved by *Acanthopagrus butcheri* in the Wonnerup Inlet from the best fitting Generalised additive mixed model. N.B. the two modal peaks in movement activity at days ~80 and 170 of the study.

4. Discussion

The impact of anthropogenic barriers in rivers and estuaries on diadromous fishes, particularly salmonids, is relatively well documented (Swanson et al., 2013; Pess et al., 2014), however, the current study is the first to elucidate the impact of an estuarine storm surge

barrier on an obligate estuarine fish at the individual level. Previous studies on *A. butcheri* have found that salinity and spawning activity were the key drivers of the movement and seasonal distribution (Hindell et al., 2008; Sakabe and Lyle, 2010; Williams et al., 2017). Despite the Vasse-Wonnerup Estuary being highly regulated and of a much smaller size than the estuaries studied previously, many of the key factors driving movements here are broadly consistent with those studies albeit with some notable differences. The results of the current study also suggest the Vasse surge barrier is likely to be exacerbating the severity of recent fish kill events by interacting with the biological and environmental factors driving the movement and distribution of *A. butcheri*.

Peak spawning of *A. butcheri* in the Vasse-Wonnerup occurs between August and October; which is earlier than in the more northerly Swan-Canning Estuary in south-western Australian where peak spawning usually occurs between October and December, but is similar to the southerly Wellstead Estuary further to the east (Sarre and Potter, 1999). The results of the current study suggest that the Vasse surge barrier is likely to impede the upstream movement of the species during the spawning period; as demonstrated by clear increases in the daily number of fish detected at the receiver downstream of the barrier during that period. Despite this congregation, only two fish traversed the surge barrier when it was pushed open by flows at the initial onset of the flow period. It is possible that the hydrological conditions may have exceeded the species' swimming performance capacity for the majority of the high flow period (noting that no literature is available on the swimming performance metrics for this species). However, access to habitat upstream would provide little potential benefit to the population. Firstly, there is a relatively small amount of suitable habitat available upstream of the Vasse surge barrier; particularly during the warmer period when water levels decline (Fig. 1). Secondly, *A. butcheri* are known to congregate at estuarine haloclines to optimise its reproductive success through increasing larval survival (Williams et al., 2012). While salinity profiles were not taken during the current study, the surge barriers clearly nullified tidal influence at the sites upstream (Supplementary Figs. 11 and 15) thus this habitat would likely have been unsuitable for spawning and recruitment. The Vasse surge barrier was therefore not preventing access to spawning habitat, rather, it is creating a one-way trap by restricting a considerable proportion (~29% in the current study) of the adult population of *A. butcheri* within the key fish kill zone, which has considerable implications for the management of the structure.

The results of the current study help to explain why the more recent fish kills have occurred within the proximity of the Vasse surge barrier and have reported to be predominately *A. butcheri* and two mugilid species. While 20 species of fish have been recorded in the offshore waters of the Vasse-Wonnerup, only two mugilid species have been caught upstream of both surge barriers by gillnetting along with *A. butcheri* upstream of the Vasse surge barrier; with the other species being restricted to habitats downstream of the barriers in the Wonnerup Inlet (Tweedley et al., 2014). While smaller-bodied atherinids and gobies are also present upstream of both surge barriers (Tweedley et al., 2017b), their ability to move to the very shallow habitats further upstream in the Vasse and Wonnerup estuaries would enable them to avoid the seasonal severe decline in water quality in the habitat upstream of the surge barrier. Moreover, smaller-bodied species would also be less visible during a fish kill and thus may be underrepresented in reporting compared to the larger bodied *A. butcheri*.

Surge barriers can lead to upstream waters that are stagnant, eutrophic and generally poorly flushed, and can experience higher temperatures, lower dissolved oxygen, lower pH, lower salinities and a less natural fauna compared to waters downstream of such barriers (e.g., Johnston et al., 2005). The lack of fish kills occurring upstream of the Wonnerup surge barrier may be attributed to the habitat there being very shallow (~ < 1 m) thus reducing the likelihood of stagnant, stratified conditions being created. The habitat in the tidally influenced

Wonnerup Inlet is also relatively shallow (mean depth = 0.8 m, maximum = 2.4 m, [Supplementary Fig. 16](#)) and also does not experience severe hypoxia. By contrast, water quality monitoring in the main fish kill zone upstream of the Vasse surge barrier has detected prolonged periods of stratification, hypoxia and formation of toxic algal blooms ([Tweedley et al., 2014](#)). This effect is comparable to the localised (100 m) hypoxic zones formed upstream of surge barriers in the lower Fraser River, British Columbia that was believed to exclude sensitive species or create a chemical barrier to connectivity ([Gordon et al., 2015](#)).

Along with the lethal effects of hypoxia, it can have substantial sub-lethal biological effects ([Kramer, 1987](#); [McNatt and Rice, 2004](#); [McNeil and Closs, 2007](#); [Flint et al., 2015](#)). [Cottingham et al. \(2014, 2016\)](#) attributed the observed declines in growth rates, body condition, and size at maturity of *A. butcheri* the Swan Canning Estuary (Western Australia) between 1993–95 and 2007–10 to increased hypoxia in the system that had resulted in both habitat compression (to shallower waters) and a change to a lower calorie diet. Therefore, should the entrapment of a large proportion of *A. butcheri* upstream of the Vasse surge barrier be occurring annually, along with increasing the risk of large numbers of fish dying, there may be sub-lethal effects such as forcing fish to live in sub-optimal habitat and conditions potentially resulting in reduced growth rates.

Mean daily movement rates by *A. butcheri* in the current study were $2.3 \pm 0.06 \text{ km.day}^{-1}$, which was similar to that recorded by [Hindell et al. \(2008\)](#) for *A. butcheri* in the Gippsland Lakes, Victoria, Australia ($2.7 \pm 0.40 \text{ km.day}^{-1}$) and by [Williams et al. \(2017\)](#) within its two estuaries (1.7 km.day^{-1} and 2.1 km.day^{-1} for the Mitchell and Tambo estuaries, respectively). While [Sakabe and Lyle \(2010\)](#) found that tide influenced smaller scale movements of this species, the current study revealed no influence of tidal amplitude on its daily movement. However, estuaries in this region are microtidal, including the Vasse-Wonnerup system (maximum 1.01 m) ([Hodgkin and Hesp, 1998](#); [Tweedley et al., 2016a](#)), and it is likely that a low tidal amplitude explains the lack of influence on the species. [Williams et al. \(2017\)](#) also found no influence of tidal movement on the species in a microtidal system in south-eastern Australia. The opening of the surge barrier during winter and spring due to river discharge positively affected the amount of daily movement of the species. Freshwater flow has previously been shown to influence the movement of the species being the cue for large downstream movements ([Williams et al., 2017](#)). [Sakabe and Lyle \(2010\)](#) revealed that rainfall and fresh flow during the spawning period caused a downstream movement of the species; thereby potentially interrupting spawning activity that typically occurs in upstream reaches of estuaries ([Hindell et al., 2008](#); [Williams et al., 2012](#)). However, no such downstream movement was recorded during the current study, on the contrary, fish tended to congregate upstream below the Vasse surge barrier during peak flows possibly as a result of these coinciding with its earlier winter-spring breeding period in this regulated system; also noting that the rainfall during the study period was highly seasonal ([Supplementary Fig. 17](#)).

The study has implications for the management of the Vasse surge barrier and other instream barriers that intersect the habitat *A. butcheri* throughout its range in southern Australia. Despite *A. butcheri* being considerably mobile and undertaking upstream spawning migrations, there is little evidence to suggest that they utilise fish passage devices in eastern parts of southern Australia ([Baumgartner et al., 2014](#); [Bice et al., 2017](#)). For example, [Mallen-Cooper \(1996\)](#) concluded that *A. butcheri* had an inhibition to pass through restricted spaces such as tunnels and [Bice et al. \(2017\)](#) also found that this species did not successfully negotiate fishways. The current study recorded successful upstream passage only on days where a negative head differential from downstream to upstream was recorded. This suggests that the species may have limited propensity to passage against the flow through artificial structures. Therefore, this limits the effectiveness of fish passage devices that aim to increase the habitat availability for the species;

including in situations where passage away from undesirable habitat conditions is necessary.

A combination of both field and laboratory studies may be key to fully understanding the effectiveness of fish passage devices. [Tummers et al. \(2016\)](#) highlighted the efficacy of undertaking complementary acoustic and passive integrated transponder (PIT) tagging studies to demonstrate the ineffectiveness of a retro-fitted fish passage device in Britain in enabling passage of the European Lamprey *Lampetra fluviatilis*. In order to determine the precise hydrological conditions by which passage through the Vasse surge barrier occurs, a PIT reader system should be similarly incorporated along with complementary modelling of hydrological conditions within the fishgate that would enable elucidation of the hydrological conditions for fish passage. Such a study would also enable experimentation with the management of the fishgate to enable downstream movement through the barrier in summer and autumn. No valid detections of *A. butcheri* were recorded upstream of the Wonnerup surge barrier during the current study despite it being of the same design as the Vasse surge barrier. The height of the fishgate opening on the Wonnerup surge barrier was much less than the Vasse surge barrier for the duration of the study ([Fig. 3](#)) and thus may not have enabled passage through the barrier for the deep bodied *A. butcheri* while the shallow-bodied mugilids, known to occur upstream of the Wonnerup surge barrier, may have been able to traverse through the fishgate. The study revealed a minimum gap height of the Vasse fishgate opening that a passage event occurred during the current study was 11.7 cm, therefore providing that gap as a minimum under certain hydrological criteria (e.g. under minimum head difference across the barrier that would occur on low tides) may provide an opportunity to mitigate the effects of the Vasse barrier on this species, and potentially also enable passage through the Wonnerup surge barrier. Moreover, laboratory derived burst and prolonged swimming performances metrics should be determined that could then inform the design of retrofitting devices on these and other barriers; such as Larinier super active baffles ([Larinier et al., 2002](#)). While we focussed on *A. butcheri* as the model species given its vulnerability to fish kills in this system and its value as a target of recreational fishers, a similar understanding of the movement of other resident or diadromous species through both the Vasse and Wonnerup surge barriers is also warranted.

Climate change will increase the need for protection of human developed low-lying land and thus surge barriers in estuaries may become increasingly important ([Hallett et al., 2018](#)). For example, sea level in this region is predicted to increase by 28–66 cm by 2090, under RCP4.5 ([Hope et al., 2015](#)) and this will increase the susceptibility of estuaries to coastal flooding ([Hallett et al., 2018](#)). It is projected that a 50 cm increase in mean sea level in south-western Australia will result in a 100 to 1000 – fold increase in the frequency of extreme sea level events ([Braganza et al., 2014](#)). Moreover, increased sea level in conjunction with the concomitant ongoing reductions in freshwater discharge owing to reduced annual rainfall have considerable implications for estuarine fishes. For example, changes in the fish communities of the nearby Swan-Canning and Peel-Harvey estuaries were attributed, in part, to a more marine-like environment having developed over a period of dramatic climate shift ([Potter et al., 2016](#); [Valesini et al., 2017](#)). The synergistic impact of climate change with the human response of installing surge barriers to combat its effects therefore have profound implications for estuarine fishes; particularly those that migrate as part of their life-cycle.

5. Conclusion

The study underlines the importance of understanding the biology and ecology of resident fishes during the design and operation of estuarine surge barriers. Determining the biological and environmental drivers of the movement and distribution of *A. butcheri* in the Vasse-Wonnerup Estuary has revealed that the Vasse surge barrier was impacting the species; not by restricting access to suitable foraging or

spawning grounds as is often intuitively the case for diadromous species such as salmonids, but by restricting movement of the species away from sections that seasonally experiences depleted water quality. Design and operation of estuarine surge barriers should consider not only their hydrological aims, but also the nuances of their potential ecological impacts at the local scale. Understanding the movement and life-cycles of both estuarine and diadromous species will help underpin effective design and operation of estuarine surge barriers. Ensuring their effectiveness in both protecting coastal development and minimising their ecological impact is paramount given they will likely become increasingly used in many regions to protect against coastal storm surges and flooding under projected climate change scenarios.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ecoleng.2018.07.009>.

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